# THE HOLACANTHOID PLANTS OF NORTH AMERICA

Cornelius H. Muller

One of the striking botanical phenomena of the southwestern United States and adjacent Mexico is the occurrence of several genera of different families with vegetative characters so similar as to make them confusing. Perhaps the most outstanding such instance is that of the usually leafless green spiny shrubs which resemble *Holacantha Emoryi* A. Gray, a member of the Simarubaceae. The similar forms are *Koeberlinia spinosa* Zucc. in the Koeberliniaceae, *Canotia holacantha* Torr. in the Celastraceae, and *Thamnosma montana* Torr. & Frem. in the Rutaceae.

These four species are characterized by leaves reduced to scales and early caducous, and spinescent stems persistently green to carry on the photosynthetic process. The lack of leaves and similarity of the spines make these plants rather difficult to distinguish without flowers or fruit. Yet, a series of vegetative characters may be recognized by which the species are readily distinguished.

There are other spinescent plants which might be confused with the group here treated. The others, however, are characterized by shorter and more slender spines and usually more prominent leaves. For instance, *Adolphia* in the Rhamnaceae and *Forsellesia* in the Celastraceae contain species highly similar in habit to the Holacantha-like plants, but in these the spines do not exceed an average of 2.5 millimeters in thickness, and the leaves are prominent throughout the greater part of the growing season. Furthermore, *Adolphia* is characterized by opposite leaves and branches, while those of the plants here treated are all alternate. Two variants of *Koeberlinia spinosa* have been distinguished under varietal names. Both of these are characterized by very slender spines which might make them difficult to distinguish from *Adolphia* except for their alternate habit of branching. Leafless individuals of the leguminous shrubs *Cercidium* and *Cassia armata* might become confusing when they lack flowers and fruit.

The highly artificial group comprised of the Holacantha-like plants is characterized by the alternate-branching, spinescent stems, the spines usually quite coarse, branches green and photosynthetically functional for several years, leaves much reduced and early caducous. Johnston (Journ. Arn. Arb. 21: 356–363. 1940) has pointed out the significance of this group of unrelated plants of similar habit as indicative of a relationship between the North American deserts and those of South America where the same habit is common. He showed the habit to be much more general in the South American deserts than in North America. The highly endemic character of all our species except *Koeberlinia spinosa* would indicate that the plants are relicts of a time when the habit was more common in North American deserts.

KEY BASED ON VEGETATIVE CHARACTERS

Leaf scars and branching alternate, leaves inconspicuous and early caducous.
- Plants glabrous, stem either densely glandular or with minute longitudinal lines of white waxy flakes.
  - Stems densely glandular or warty with translucent glands; buds and spine tips tan; branches with a pair of extra-axillary buds at the bases (one on each side) ..... *Thamnosma*
  - Stems not glandular, with minute longitudinal lines of white waxy flakes; buds dark brown or black, spine tips brown; branches with no extra-axillary buds *at* the bases (though the buds along the length of the branch may descend to a point *near* the base) ..... *Canotia*
- Plants with young stems pubescent, neither glandular nor with waxy exudations.
  - Younger stems yellow-green, minutely puberulent with short spreading hairs or these reduced to pustules; branches and spines with a pair of buds at the bases, these extra-axillary (one on each side) ..... *Koeberlinia*
  - Younger stems gray green with densely matted appressed silky hairs; branches and spines with a single axillary bud and no lateral or extra-axillary buds at the bases .. *Holacantha*

Leaf scars and branching opposite or, if alternate, the leaves conspicuous and persistent . . . (genera not treated in this article).

THAMNOSMA MONTANUM Torr. & Frem. in Frem., Rep. Exped. Rocky Mts. 313. 1845.

Central Arizona north to southwestern Utah, southern Nevada, and southern California; most common in western Arizona. A shrub usually 3 to 6 or 7 decimeters tall. (fig. 1).

CANOTIA HOLACANTHA Torr., U. S. Rep. Survey Railroad Miss. Pac. 4: 68. 1856.

Southeastern and central Arizona to northwestern Arizona and doubtfully in the Providence Mountains of southeastern California. A shrub 3 to 5 or even 6 meters tall. (fig. 2.)

KOEBERLINIA SPINOSA Zucc., Abh. Akad. Muench. 1: 359. 1832.

Southern Arizona and New Mexico, western Texas, Baja California, northern Sonora and Chihuahua, south through Coahuila and Nuevo Leon to Puebla and Oaxaca. A shrub 0.5 to 2 meters or even a small tree to 5 meters tall. (fig. 1.)

KOEBERLINIA SPINOSA var. TENUISPINA Kearney & Peebles, Journ. Wash. Acad. Sci. 29: 486. 1939.

Yuma County, Arizona, and Sonora, Mexico. Differs from the species in its elongate slender spines, blue-green color, and usually longer sepals, petals, and filaments. Typical *K. spinosa* apparently occurs nowhere west of Tucson, Arizona. This variety is not distinguished from the species on the distribution map.

A second variety (*K. spinosa* var. *verniflora* Bogusch, Torreya 31: 74. 1931) now scarcely seems worthy of distinction. Although this form differs strikingly from the species by its slender spines (and generally reduced size of the organs) and its early flowering (in March and April), its differences are not sufficiently profound nor constant to warrant formal recognition. Nor is

Figs. 1 and 2. Distribution of holocanthoid plants in southwestern North America.

there any geographical segregation from the species. The morphological basis of this form has been observed by the author in various parts of western Texas and adjacent Chihuahua and Coahuila. In a letter to the author under the date October 7, 1940, Bogusch discusses the variety as follows: " . . . observations made in the field upon specimens of *Koeberlinia spinosa* Zucc. convince me that the variety *verniflora* described by me is probably a normal reaction of the plant to wound stimulus or represents a form of juvenile growth. From material seen both in the type locality of the Rio Grande Valley of Texas and in the region west of Uvalde, I have seen that new growth which follows extensive injury to the plant often results in being more attenuated, both in branches and the spines. The peculiarities associated with the time of flowering—not necessarily a taxonomic character—may be best explained that in the Rio Grande Valley the vegetation in many respects matures earlier and comes into flower sooner than elsewhere in the state."

Holacantha Emoryi A. Gray, Mem. Am. Acad. ser. 2, 5 (Pl. Nov. Thurb.): 310. t. 8. 1855.

Central and southwestern Arizona to southern California. A shrub 1 meter tall to a small tree reaching 3.5 meters (fig. 2).

An undescribed species of *Holacantha* was recently discovered in northen Mexico.

**Holacantha Stewartii** sp. nov. Frutex procumbens vel adscendens 1.5–3(6) dm. altus duplo latior; spinae plusminusve appresso- vel patenti-pubescentes glabratae, papillis minutis exceptis; fructus acutus margine ventrali obtuso-costatus.

Low shrub, 1.5–3 dm., rarely 6 dm. tall, usually 2–4 times as broad, procumbent or somewhat ascending, soon leafless, coarsely spiny; stems and spines divaricate; spines 2.5–6(12) cm. long, (1.5)2.5–3 mm. thick, tips subulate, brown, 3–4 mm. long, branches terete, the immature ones becoming sulcate in drying, glabrate or somewhat spreading-pubescent or appressed-sericeous, hairs short, bases persisting as minute papillae; buds inconspicuous in axils of spines and sparsely scattered along their length, surrounded by small tufts of coarse appressed hairs; leaves quickly deciduous, oblong, acute at both ends, sessile, 5–8 mm. long, 2–2.5 mm. broad, red at vernation (as are the young spines for a time), densely white- or rose-hirsute, becoming green and sparsely hirsute; flowers dioecious; staminate calyx of 6 ovate, acute, pubescent sepals about 1 mm. long; corolla of 6 fleshy, dorsally pubescent, deeply concave petals with narrow, thin margins, 4 mm. long, 1.75 mm. broad (not flattened), stamens about 12, filaments 1.5–2 mm. long, broadened basally, strongly hirsute, apex subulate, glabrous; pistillate calyx similar to the staminate; pistillate corolla not seen; staminodes similar to the functional filaments; carpels distinct, apically connivent, stigmas sessile, fused; fruit persistent 1–2 years, 6-carpellate (or carpels fewer

by abortion), carpels distinct, divaricate, lenticular-ovate, acute, ventral margins obtusely ridged, superior, 8–9 mm. long, 5–6 mm. broad, 3–4 mm. thick, glabrous, red or green, surface nearly smooth, lacquered. (fig. 2.)

Range: Mexico; western Coahuila and northern Zacatecas.

*Holacantha Stewartii* is named in honor of Mr. Robert M. Stewart of Santa Elena, Coahuila, whose superior hospitality and whose company on several side trips contributed markedly to the pleasure and success of the several weeks' work in the vicinity.

This species is the second described in this rare and striking genus, the first being *Holacantha Emoryi* which is confined to Arizona and California. From that species *H. Stewartii* differs in its low sprawling habit, the sparse pubescence of its stems (compared with the densely short-tomentose stems of *H. Emoryi*), the persistence of papillae-like hair-bases, and its usually markedly acute and ventrally ridged carpels. The great discrepancy in the ranges of these two endemics further attests their distinctness.

Specimens examined. Coahuila: Sierra de las Cruces, gulch in limestone hills 0.5 mile north of Santa Elena, August 13, 1940, *I. M. Johnston & C. H. Muller 215* (United States National Arboretum, USNA, type, sheet no. 96733; Arnold Arboretum, AA); southeast base of Sierra de las Cruces, 3 miles northeast of San José, September 5, 1940, *I. M. Johnston & C. H. Muller 1003* (AA, USNA); north base of Sierra de las Cruces, at San Rafael, September 8, 1940, *I. M. Johnston & C. H. Muller 1034* (AA, USNA); northwest base of Sierra de las Cruces, at San Vicente, September 8, 1940, *I. M. Johnston & C. H. Muller 1065* (AA, USNA); 3 to 5 miles south of Laguna de Jaco, September 10, 1940, *I. M. Johnston & C. H. Muller 1104* (AA, USNA); north end of Bolson de los Lipanes between El Almagre and Cerros de Leja, September 12, 1940, *I. M. Johnston & C. H. Muller 1239* (AA, USNA). Zacatecas: banks of arroyos in foothills, Hacienda de Cedros, 1908, *F. E. Lloyd 191* (United States National Herbarium).

With the exception of the type collection and Lloyd's from Zacatecas all the plants collected or observed grew in deep, heavy silt flats, usually associated with *Koeberlinia spinosa* Zucc. Although the most luxuriant growth and fruiting occurs in rocky arroyo sites, the species is obviously more at home in the former habitat, as is evidenced by its more frequent occurrence there. The plant is often the only one (or one of a few) on otherwise bare silt. Its procumbent habit serves to bind the soil and forms hillocks down the sides of which the branches sprawl.

In two of the seven collections studied fasciated stems were noted. These are flattened and falcate with two ranks of simple normal spines issuing from their edges. It is odd that two such cases of identical abnormality were encountered in so rare a plant, about fifty individuals being observed in the course of a wide and painstaking search.

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